

STUDIES ON THE STRUCTURE AND
TAXONOMY OF *BULINUS JOUSSEAUMEI*
(DAUTZENBERG)

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STUDIES ON THE STRUCTURE AND TAXONOMY OF *BULINUS JOUSSEAUMEI* (DAUTZENBERG)

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SYNOPSIS

Many recent workers on the freshwater mollusca of Africa have tended to present synonymies based more on the literature and on personal opinions than on a study of the animals themselves. This is particularly true of those gastropods of medical importance which act as intermediate hosts for flukes parasitizing human beings. This paper is an attempt to establish the relationships of one such snail.

HISTORICAL

DAUTZENBERG (1890) described *Bulinus jousseaumei* as a member of the genus *Isidora* and stated that it belonged to the *I. contorta* group with a strong affinity to *I. natalensis*. Pilsbry & Bequaert (1927) list *B. jousseaumei* in the sub-genus *Bulinus* s. str. and Amberson and Schwarz (1953) place it in the synonymy of *B. truncatus*. I have shown that both on conchological and anatomical grounds the species is properly placed in the sub-genus *Physopsis* (Wright 1956). Smithers (1956) has shown that in parts of the Gambia Protectorate this snail is an important vector of the human blood-fluke, *Schistosoma haematobium*. From personal observations I am sure that it is also the vector implicated in the Casamance Province of Senegal by Deschiens (1951) under the name *Bulinus trigonus*, a species characteristic of some lakes in East Africa.

MATERIAL AND METHODS

The material of *B. jousseaumei* from the Gambia and Senegal used in this work was collected personally, in collaboration with S. R. Smithers. Material from other localities has mostly been seen in the collection of the British Museum (Natural History) or has been sent to me by other workers.

Shell measurements were made with an eyepiece micrometer in a binocular dissecting microscope, the shells were held steady in a horizontal position by means of a piece of plasticine on the microscope stage. Radula preparations were made following the rapid methods recommended by Meeuse (1950).

THE SHELL

The original description of the shell by Dautzenberg is very adequate and my re-description (Wright, 1956) adds little to the original, apart from noting a further colour variation from light yellowish-straw to dark reddish-brown, and amplifying

the details of the ornamentation. Since reference will be made later to the sculpture my previous observations are repeated here. There is a regular punctate pattern on the nuclear whorl and the rest of the shell is covered with fine growth lines superimposed on which is a delicate pattern of short, wavy, vertical lines. It is surprising that Dautzenberg, who must have been acquainted with *Physopsis*, was so definite about the affinities of *B. jousseaumei* in spite of his mention of the twisted base of the columella in his description.

One of the greatest difficulties in the description of gastropods is the definition of size. The old workers when describing a new species usually gave the dimensions of the specimen (often the largest) which they had selected as the holotype. Rarely, they gave the dimensions of the largest and the smallest specimens available to them. The dangers of this approach to the problem in an animal which grows steadily without a well-defined adult phase are obvious. Size ranges are valueless since they give no idea of distribution, and ranges given with a mean and standard deviation are not of much use unless the growth stages represented in the sample are known. The ratios of certain measurements of the shell are of more value but these may vary with shell length. For instance Peters (1938) has shown that the ratio shell length/aperture length increases with shell length in *Lymnaea palustris*. Hubendick (1951) using smaller samples suggests that there is no significant change in the ratio aperture length/shell length $\times 100$ in *Lymnaea peregra*.

In order to investigate the relationships of *B. jousseaumei* it has been found necessary to analyse the size composition of various samples. The largest of these samples was collected at a washing place in the Simoto Bolon near the village of Diabugu Basilla, Upper River Division, Gambia on the 4th March, 1955. Two-hundred and thirty-eight shells were measured and spirit material dissected to try to determine an approximate correlation between shell size and the attainment of the "adult" condition. The results obtained from a study of this sample appear to be characteristic for the other samples collected in the Gambia at the same time. The time of year at which a sample is collected is of great importance since it is almost certain that the population early in the wet season contains a much higher proportion of juveniles than it would some months after the end of the rains, the time when the material under consideration was collected. Text-fig. 1 is a size frequency histogram of this sample, based on shell length. It is obvious that the greatest frequency occurs in the 8.0-9.0 mm. shell length group and the mode of the graph is at the 8.5 mm. level. The graph is, however, asymmetrical due to an overweighting of the lower size groups, the mean shell length of the sample is therefore less than the modal length. The graph does not provide any indication of whether the mode is due to large numbers of adults or juveniles and this can only be determined by anatomical study. It will be shown later that it is in the size group 6.0-7.0 mm. shell length that the accessory reproductive glands reach a fully functional stage of their development and this is taken as the beginning of the adult phase of life. If the curve showing distribution on the upper side of the mode in Text-fig. 1 is drawn and its mirror image is reproduced on the low side a normal distribution curve is formed, the lower end of which coincides well with the known onset of the adult phase. If the frequency distribution is plotted on arithmetical probability paper following the

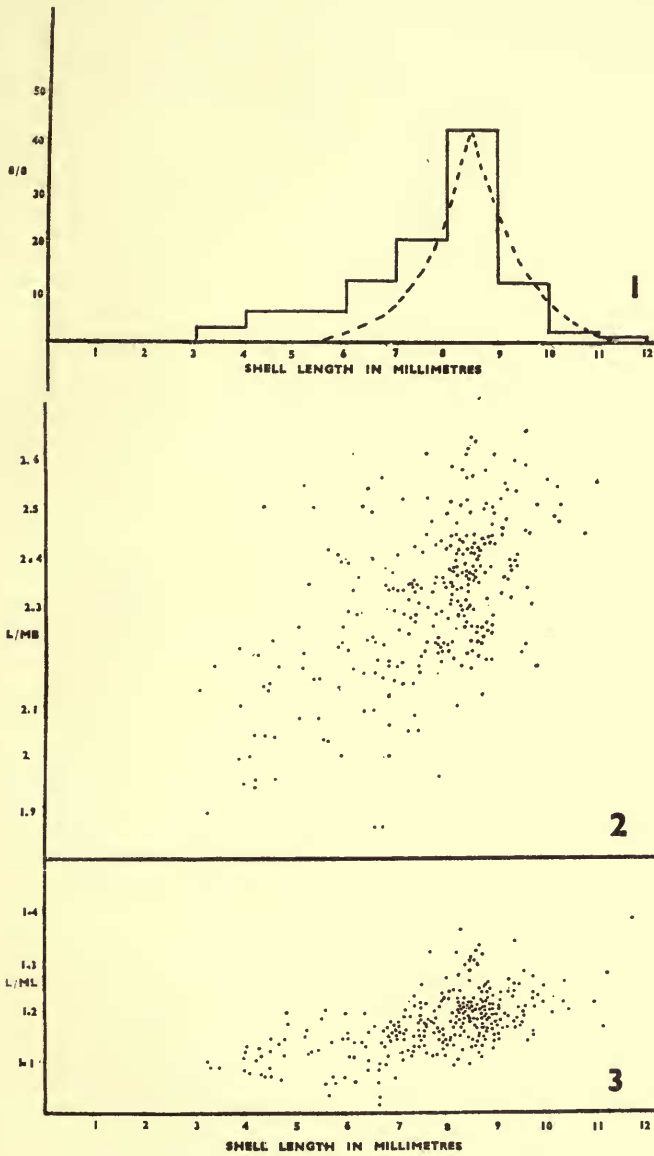


FIG. 1. Size-frequency histogram for a population of *B. jousseaumei* from the Gambia.

FIG. 2. Graph of ratio shell length/aperture width against shell length for Gambian population of *B. jousseaumei*.

FIG. 3. Graph of ratio shell length/aperture length against shell length for the same population.

method of Harding (1949) a curve is obtained which appears to be too complex to be analysed by the usual methods. This may in part be due to faulty sampling but is also undoubtedly caused by the complicated structure of a population of fresh water snails. There may be present the representatives of several successive generations, a few senescent survivors of previous generations, the adults of the present and the progeny of these adults. If the breeding season is continuous then a smooth curve might be expected but there is reason to believe that breeding is somewhat spasmodic in the bulinids and this might help to account for the complex composition of the population. Since the anatomical findings confirm that the mode of the histogram in Text-fig. 1 is in fact the mean of the adult part of the population it seems justifiable to accept 8.5 mm. as the mean shell length of the adults in this sample. An indication of the proportion of juveniles in the whole sample is given by the index of skewness, (mean-mode)/standard deviation. Having obtained a rough mean length for the adults in the population the adult means for the other dimensions may be calculated by increasing the population mean by the same percentage as that by which the mean population length differs from the adult mean length. The following table gives the mean shell dimensions of the population in millimetres and their standard deviations together with the approximate adult dimensions and the maximum sizes observed.

	Length		Max. diam.		Aperture length		Aperture width	
	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
Whole population	7.84	±1.52	6.00	±1.12	6.65	±1.03	3.37	±0.66
Adults	8.5	—	6.50	—	7.2	—	3.65	—
Maximum	11.8		8.0		9.0		4.5	

Passing from the absolute dimensions of the shells to the ratios of some of these dimensions to one another, one is faced with a number of these proportions from which to choose the most useful. Hubendick (1951) pointed out that the selection of measurements in any particular case should be made with advance knowledge of the variation to be studied. In this study of *B. jousseaumei* the object of interest is not so much phenotypic or genotypic variation as changes in form during growth. With this in mind the two ratios chosen are those of shell length/aperture length (l/ml) and shell length/aperture width (l/mb). The first of these in this type of shell gives an indication of the exertion of the spire for if the spire is strongly depressed the ratio will approach unity and will increase with the exertion of the upper whorls, or, more properly, the descent of the body whorl. The second of the two ratios expresses the relationship between the increase in diameter of the body whorl with increasing shell length. A similar result might easily be obtained by using the ratio shell length/shell diameter but with the technique of measurement employed the width of the aperture was more accurately obtainable than the maximum diameter of the shell. Text-figs. 2 and 3 show these two ratios plotted against shell length; in both it can be seen that there is an increase in the value of the ratio with increasing shell length. The change in the values is so slight that the means of the ratios provide a good index of shell form. The graph l/ml plotted against shell length

(Text-fig. 3) shows an interesting feature. For small shell lengths the graph is practically a straight line parallel to the horizontal axis and the upward slope only becomes apparent after the 6.5 mm. shell length mark. As pointed out earlier, this is the approximate shell length at which adult anatomical characters become developed and the change in form of the shell at this point is, presumably, a reflexion of the anatomical changes. The actual change in form which the shell exhibits may be explained thus: in its early stages the spire is completely depressed, subsequent whorls being added around the preceding ones; at the onset of maturity the accessory genital glands increase in size very rapidly necessitating an increase in shell volume to accommodate them and this is achieved by the body-whorl moving downward in relation to its predecessor, giving an increase in shell length without a corresponding increase in aperture length.

The means and standard deviations of these two ratios in the population under consideration are

l/ml	mean 1.17	s.d.	± 0.08
l/mb	mean 2.31	s.d.	± 0.143

THE MANTLE

The mantle markings of *B. jousseauimei* from the Gambia consist of patterns of small black spots and patches scattered irregularly over a light grey field. The spots often appear dark grey rather than black owing to the pigment granules of which they are composed being only loose aggregations rather than dense concentrations.

The nephridial ridge on the underside of the mantle may be well developed or almost absent. It is often present only on the distal end of the kidney. The intermediate ridge is almost always well developed and is about equal in length to the kidney. An examination of transverse sections of the mantle has failed to show the presence of ciliated epithelium on this intermediate ridge (described for *B. africana* by Hubendick, 1948) but this may be due to the method of fixation employed.

THE RADULA

The radula is in no way remarkable. The number of tricuspid laterals varies from six to eight in each transverse half-row. This number does not appear to change with the age of the snail, but the number of marginal teeth does appear to increase in older specimens. It is perhaps worthwhile recording here that the first lateral tooth is tricuspid (Text-fig. 4). Dupuis and Putzeys (1923) mention as the only real difference between *Physopsis* and *Isidora* that the first lateral in the former group is bicuspid while in the latter it is tricuspid. The endocone of the first lateral is often difficult to observe and it is doubtless this fact that gave rise to the erroneous statement of these authors.

CENTRAL NERVOUS SYSTEM

The central nervous system in the Planorbidae shows little variation between the various genera. The connectives between the ganglia are relatively long in *B. jousseauimei*, but since the material on which these anatomical observations are

based was all narcotized and well extended such details may not be strictly comparable with those of other workers (Text-fig. 5).

The penial nerve appears to be a composite structure with its main source in the left cerebral ganglion ; a number of other fibres running with the main component arise from the left pedal ganglion. The cerebral part of the nerve branches off from a larger trunk arising near the origin of the left cerebro-buccal connective and passing forwards giving off finer branches to the sides of the head and lips. It is probable that the nerves arising from the cerebral ganglia have a primarily sensory function, while those from the pedal ganglia are mainly motor. This would mean that the composite nature of the penial nerve provides both sensory and motor innervation for the copulatory organ. The principal nerve arising from the dorsal surface of each of the cerebral ganglia runs to the tentacle, its associated lobe and the eye on the same side of the body as that from which it arises. The pedal ganglia send several large nerves down into the foot and running back from the two buccal ganglia is a pair of fine nerves, one on either side of the oesophagus. The three visceral ganglia send nerves to the organs in the visceral mass and one large trunk arising from the left visceral ganglion passes to the anal lobe and pseudo-branch, while a similar large trunk from the right visceral ganglion passes upwards to the mantle. Contributory evidence as to the sensory nature of the cerebral ganglia is obtained from the otocyst which, although partially embedded in the posterior side of the pedal ganglion appears to be innervated solely from the cerebral ganglion above (Text-fig. 6).

BLOOD CIRCULATORY SYSTEM

The heart lies within its extremely delicate pericardium on the mantle close to the proximal end of the kidney, above the point at which the oesophagus passes into the crop. The auricle receives blood from the very large vein running along the anterior edge of the kidney. The aorta leaving the ventricle is variable in length, it may pass right over the intestinal loop which curves round the gizzard before dividing (Text-fig. 7) or it may divide so far back that the ventricle has a bifid appearance. In either case, the lesser of the two branches follows the intestine on its course round the gizzard while the major branch passes upward over the posterior edge of the gizzard. As it passes over the space between the intestine and gizzard a very large artery passes down between these two organs and divides almost at once, one branch going to the crop and distal side of the gizzard, the other to the accessory genital glands and the head cavity. A short distance after this division of the main branch from the aorta a smaller branch is given off to supply the stomach and proximal part of the gizzard and the rest of the vessel continues up the side of the gizzard, past the point at which the digestive gland opens from the intestine, and then, giving off a number of side branches into the digestive gland, follows the path of the intestine as it loops up into the upper whorls of the body. The principal artery to the head follows beneath the oesophagus to the circum-oesophageal nerve ring where vessels supplying the ganglia are given off ; then, after passing through the nerve ring it divides. One branch passes vertically downwards as the pedal artery and the other continues forward to the underside of the buccal mass where the

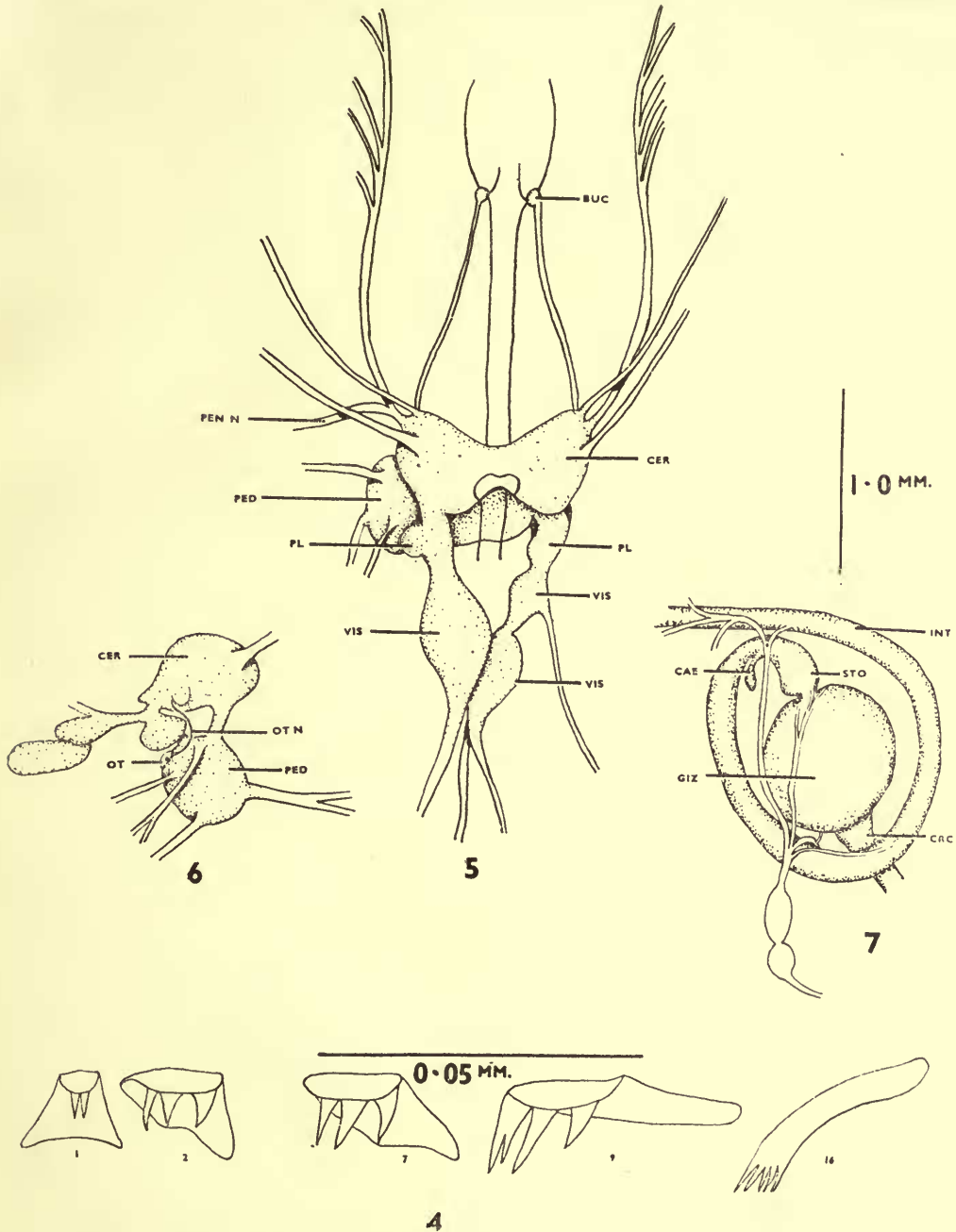


FIG. 4. Radula teeth of *B. jousseaumei* from Gambia.

FIG. 5. Central nervous system of *B. jousseaumei*.

FIG. 6. Right lateral view of central nervous system of *B. jousseaumei* to show the otocyst and its innervation

FIG. 7. Heart and principal arteries of *B. jousseaumei*.

(Figs. 5, 6 & 7 to same scale.)

vessel dilates before breaking up into fine branches supplying the muscles of the mass and the sides of the head and lips. A fine lateral branch which leaves the main trunk in the region of the nerve ring serves the penial complex. It runs parallel with the penial nerve and appears to enter the complex at the junction of the penis sheath and preputium.

ALIMENTARY SYSTEM

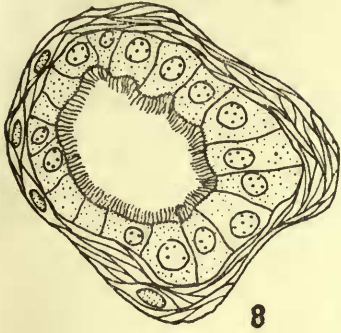
The digestive tract in the Planorbidae is so well known and subject to so little variation that it is not necessary to enter into a full description here.

REPRODUCTIVE SYSTEM

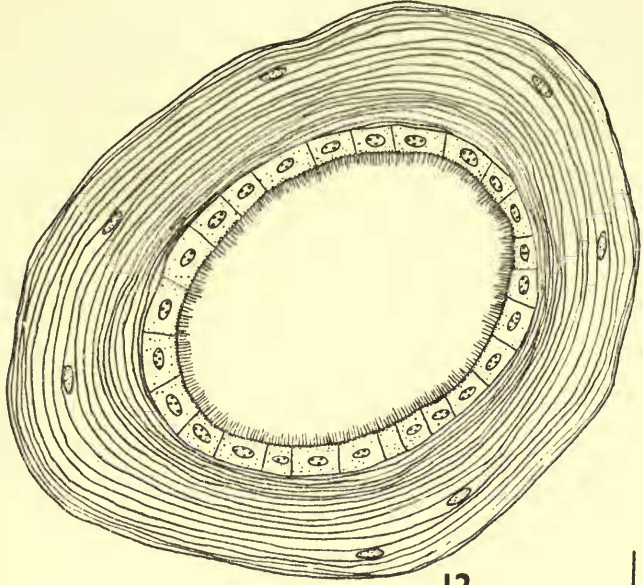
The gross morphology of the genital tract of *B. jousseaumei* has already been described (Wright, 1956). It is intended here to consider the histology of the tract and its development. Hubendick (1948 *a* & *b*) has described the anatomy and histology of the male copulatory organs of several species of *Bulinus*. Larambergue (1939) has described fully the reproductive anatomy and histology of *Bulinus truncatus*. Abdel-Malek (1954 *a* & *b*) has given detailed accounts of the morphology and histology of the genital organs of two Planorbids *Helisoma trivolvis* (Say) and *Biomphalaria boissyi* and comparisons between all of these and *Bulinus jousseaumei* will be made.

Histologically no real differences were found between Abdel-Malek's description of the ovotestis in *Biomphalaria* and *Helisoma* and that in the present species. The acini are enveloped in "Ancel's layer" of thin connective tissue and the germinal epithelium within this layer appears to line only the lower parts of the acini. Heavily pigmented connective tissue is largely confined to the layer covering the top of the organ. In the adult snail all stages of spermatogenesis and oogenesis can be observed in the same acinus. Young oöcytes and spermatids are largely confined to the lower parts of the acini and the upper parts are occupied by maturing ova, as many as six having been seen in a single acinus as compared with two to three reported by Abdel-Malek in *Helisoma trivolvis*. The mature ova are enclosed within a follicular membrane made up of nurse cells and connective tissue. Mature spermatozoa are more or less ubiquitous in the acini, either free in the lumen or attached by their anterior ends to basal "Sertoli" cells. The motility of these basal cells is shown in that they may be found on the outer wall of the follicles of maturing ova, a position that could only be reached by their independent locomotion. The hermaphrodite duct is lined with an epithelium of cuboidal cells bearing short cilia and the duct is sheathed in a thin layer of connective tissue (Text-fig. 8). The epithelium lining the seminal vesicles is similar to that in the hermaphrodite duct but the median

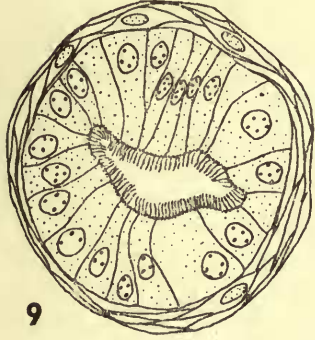
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- FIG. 8. Transverse section of hermaphrodite duct of *B. jousseaumei*.
 FIG. 9. Transverse section of first part of sperm duct of *B. jousseaumei*.
 FIG. 10. Transverse section of sperm duct of *B. jousseaumei*.
 FIG. 11. Epithelial lining of prostate tubule of *B. jousseaumei*.
 FIG. 12. Transverse section of vas deferens within body wall of *B. jousseaumei*.
 FIG. 13. Transverse section of vas deferens in head cavity of *B. jousseaumei*.



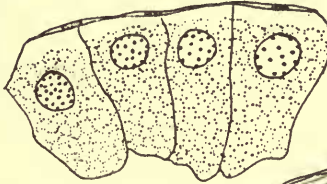
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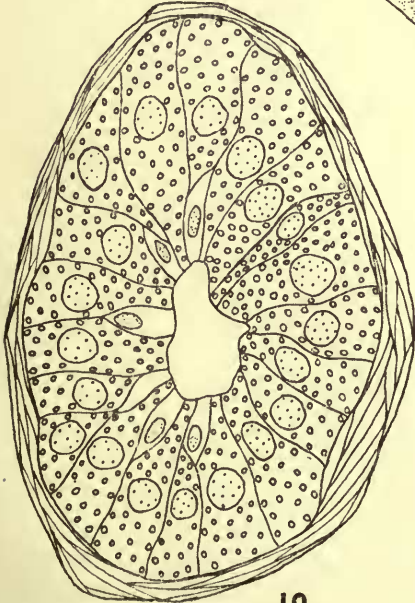


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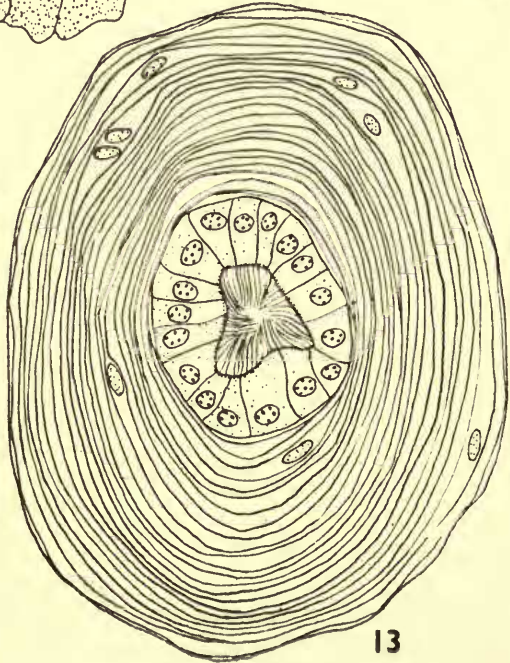


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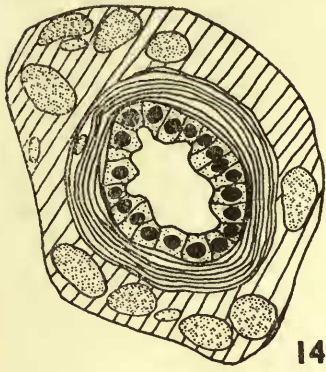
nuclei are a little larger and the cytoplasm is more granular. The separation of the male and female ducts from the common duct occurs at a point well embedded in the base of the albumen gland. The sperm duct at its source is narrow with a small lumen lined by short columnar epithelial cells, ciliated, and with median to basal nuclei and finely granular cytoplasm (Text-fig. 9). This part of the duct is quite short and it soon becomes considerably larger in diameter although the size of the lumen does not increase greatly. The epithelium lining the duct loses its cilia and the cells are of a much taller columnar type with median nuclei, larger than those in the earlier part of the duct, and the cytoplasm is filled with large, eosinophilic, refractile granules. A few wedge-shaped cells occur between the apical ends of the columnar type and these do not contain the eosinophilic refractile granules (Text-fig. 10). The sperm duct retains this histological structure right up to its entry into the prostate gland. Hubendick (1948a) in discussing the structure of the prostate in *Bulinus* has shown that in *B. inflatus*, an Australian species, the tubules of the prostate open individually into the vas deferens which enters the gland at the proximal end and leaves it distally, a structure similar to that in *Physa*. In *B. jousseaumei* however the prostate is a discoidal structure, flattened on one side and convex on the other. The sperm duct enters the gland almost in the centre of the flattened surface and the vas deferens leaves it also almost in the centre. There is therefore a central point at which the tubules of the prostate discharge their secretion into the male duct and it is at this point that the histological structure of the male duct changes from the typical form of the sperm duct to that of the vas deferens. The tubules of the prostate gland are close-packed, each is ensheathed in a thin-layer of connective tissue and is lined by large secretory cells with large basal nuclei with granular contents. The cytoplasm of these cells is eosinophilic and not granular (Text-fig. 11). There are some basophilic cells near the blind ends of the tubules. As the vas deferens leaves the prostate it is lined with sparsely ciliated epithelium of rather flattened cuboidal cells with central nuclei containing sparse chromatin granules. This epithelium is surrounded by a thin layer of circular muscle. As the duct proceeds on its course there is an increase both in the ciliation of the lining epithelium and in the thickness of the circular muscle layer. Where the duct passes through the body wall the lumen is large, the cells of the epithelial lining are wider than high, the cilia are plentiful but not long and the muscle layer is thick (Text-fig. 12). After leaving the body wall and entering the head cavity the structure of the vas deferens changes slightly. The lumen becomes more restricted, the epithelial lining more columnar, with basal nuclei, still with few chromatin granules in the clear nucleoplasm, the cilia become longer and the muscle layer thicker (Text-fig. 13). At the point of entry into the penis sheath the duct becomes the epiphallus which lies coiled in the upper part of the sheath and which has a very different appearance in section (Text-fig. 14). The overall diameter is reduced but that of the lumen remains more or less unchanged. The internal epithelium is of irregularly cuboidal cells with central nuclei and no cilia. The nuclei are densely packed with chromatin and stain deeply in haematoxylin. The epithelial layer is surrounded by a layer of circular muscle and outside this is a layer of transverse muscle and connective tissue with bundles of longitudinal muscle fibres embedded in it. The transition

from epiphallus to penis proper is gradual. Due to the mode of operation of the copulatory organ in *Bulinus* [Larambergue (1939) and Hubendick (1948b)] the part that is proximal when the organ is at rest is distal when it is erected and the distal resting part is proximal during copulation. The following description is based on resting specimens. Proximally, the lumen increases gradually, the epithelial lining becomes regularly cuboidal and the central nuclei are less deeply staining. At about the maximum diameter of the penis the lumen is partially occluded by profound folding of the lining. The epithelium is of cuboidal cells with central nuclei containing sparse chromatin granules and beneath this is a layer of connective tissue with transverse muscle fibres and blood spaces. Around this is a layer of muscle and the outer layer is of mixed muscle fibres with blood spaces and connective tissue (Text-fig. 15). The distal tip of the penis, just before the point where it unites with the penis sheath, has a tri-radiate lumen surrounded by the same sort of epithelium as before and outside this only a thin layer of circular muscle (Text-fig. 16). The penis sheath has an outer covering of a thin, flattened epithelium within which is a layer of mixed muscle fibres followed by an innermost layer of almost pure circular muscle. The lining of the preputium is thrown into a number of folds with two muscular pillars predominating. Usually only one of these two pillars extends the whole length of the preputium, the other usually fades out before the junction with the penis sheath at the upper end. The position of the pillars within the preputium coincides with the point of attachment on the outside of two series of muscle fibres that connect the organ to the body wall of the head cavity. The epithelial lining of the preputium is fundamentally of columnar or cubical cells with more or less basal nuclei. In the most proximal parts of the organ a few ciliated cells are present. Distributed irregularly are gland cells, much larger than the other components of the epithelium, with basal nuclei often displaced to one side of the cell (Text-fig. 17). The cytoplasm of these gland cells may be either coarsely granular and eosinophilic or much more finely granular and staining deeply in haematoxylin. They are often clustered together in patches and may penetrate quite deeply into the muscular layers beneath. They are more common in the upper proximal parts of the organ but in one specimen examined they were confined almost exclusively to the epithelium covering one of the muscular pillars. Beneath the epithelium is a layer of circular muscle and outside this a thick layer of mixed muscles and connective tissue with blood spaces.

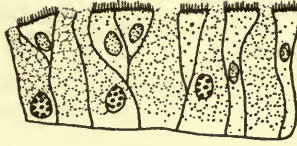
Returning to the point of separation of the hermaphrodite duct, the female tract begins with a short duct with a narrow lumen lined by columnar glandular cells with darkly-staining basal nuclei. Between the free ends of these columnar cells are wedge cells with nuclei containing few chromatin granules. These wedge cells bear short cilia (Text-fig. 18). This short duct opens into the carrefour which has a wide lumen and a folded wall. The epithelial lining (Text-fig. 19) is of tall columnar cells and wedge cells. The glandular columnar forms have dark staining basal nuclei. There are patches of ciliated cells particularly in the folds of the wall. Opening into the carrefour is the duct from the albumen gland. This gland is made up of numbers of tubules with loose connective tissue between them. The lining of the tubules is quite characteristic in section; it consists of roughly cuboidal cells

with basal granular nuclei and with numbers of large droplets in the cytoplasm. These droplets stain deeply in haematoxylin (Text-fig. 20). Distally to the carrefour the oviduct is lined with a columnar epithelium containing a few wedge cells and a few gland cells but without cilia (Text-fig. 21). The oviduct leads into the uterus which is elongate transversely in cross section. The epithelial lining is similar to that of the oviduct but there are more gland cells, some with acidophilic and some with basophilic granules in the cytoplasm. There are also a few ciliated cells (Text-fig. 22). For a considerable part of its course the uterus is surrounded by the muciparous gland. Macroscopically this gland is smooth, colourless and rather translucent in appearance. In section it is seen to be made up of close-packed tubules with little intervening connective tissue. The tubules are lined with large, irregularly cubical cells with darkly staining basal nuclei. The cytoplasm is entirely without granules and is completely unstained by either haematoxylin or eosin (Text-figs. 23). The tubules open individually into the dorsal side of the uterus. Following immediately after the muciparous gland the uterus passes into the oöthecal gland, distinguished macroscopically by its opaque white appearance in contrast to the translucent colourlessness of the previous gland. Internally the uterine wall is deeply folded in this region. The epithelium (Text-fig. 24) consists almost entirely of tall columnar glandular cells with basal nuclei. Both acidophils and basophils are present but the coarsely granular or eosinophilic type of cytoplasm predominates. A few patches of ciliated cells are present and the glandular cells may be several layers thick in places, penetrating deeply into the underlying connective tissue. The transition from the folded, glandular wall of the oöthecal gland to the tubular, ciliated vagina is quite abrupt. The epithelial cells in this part are of a short columnar type with median to basal nuclei containing sparse chromatin granules. The cytoplasm of these ciliated cells is very finely granular and eosinophilic (Text-fig. 25). The seminal receptacle duct which opens from the vagina is lined in its distal part (that nearest to the vagina) with a columnar epithelium with basal nuclei and finely granular acidophilic cytoplasm but without cilia. The rest of the duct lining is similar but the columnar cells are taller and ciliated. The distended sac of the

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- FIG. 14. Transverse section of epiphallus of *B. jousseaumei*.
 FIG. 15. Part of transverse section of penis of *B. jousseaumei*.
 FIG. 16. Transverse section of tip of penis of *B. jousseaumei*.
 FIG. 17. Part of epithelial lining of the preputium of *B. jousseaumei* showing basophilic and eosinophilic gland cells.
 FIG. 18. Epithelial lining of proximal part of oviduct of *B. jousseaumei*.
 FIG. 19. Epithelial lining of carrefour of *B. jousseaumei*.
 FIG. 20. Epithelial lining of albumen gland tubule of *B. jousseaumei*.
 FIG. 21. Epithelial lining of distal part of oviduct of *B. jousseaumei*.
 FIG. 22. Epithelial lining of uterus of *B. jousseaumei*.
 FIG. 23. Epithelial lining of muciparous gland tubule of *B. jousseaumei*.
 FIG. 24. Epithelial lining of oöthecal gland of *B. jousseaumei*.
 FIG. 25. Epithelial lining of vagina of *B. jousseaumei*.



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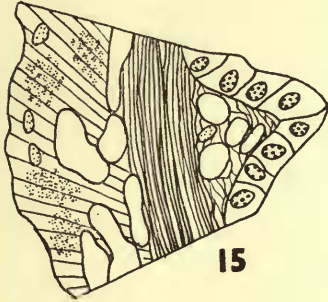
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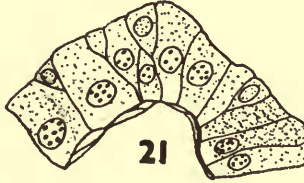
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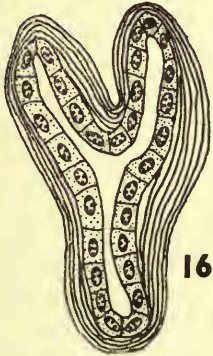


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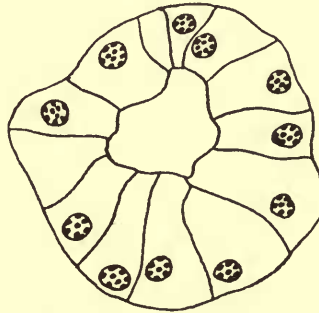


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0.05 mm.



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receptaculum is thin walled, a thin layer of connective tissue lying outside a tall columnar epithelium with basal nuclei and indistinct cell boundaries.

The foregoing description is based on a study of sections of the genital organs of several adult snails in the 8.0-9.5 mm. shell length range. For comparison series of sections were cut through the reproductive organs of a juvenile snail (4.5 mm. shell length) and an "adolescent" specimen 5.7 mm. long.

The gonad of the juvenile showed neither mature ova nor spermatozoa. Active cell division appeared to be in progress in the zone of the germinal epithelium near the bases of the acini but the state of fixation of the specimen made definite observations difficult. No sections of the haemaphrodite duct were obtained. The male tract was not clearly defined until the level of the prostate gland. This organ was present but in section the tubules although defined were lined with an undifferentiated cuboidal epithelium with central nuclei. The vas deferens leading from the prostate was lined with a similar unciliated epithelium. The sheath of circular muscle present in the adult snail was represented by close-packed undifferentiated connective tissue cells. The duct remained more or less unchanged in this condition throughout its course. The epiphallus was again ensheathed in undifferentiated tissue and the epithelial lining was of more columnar cells with basal nuclei. The penis and penis sheath at this stage also showed no clear definition of muscle tissue and the separation between the muscle layers of the two parts was just becoming apparent. The folding of the inner wall of the penis was already in evidence. The preputium also was surrounded by undifferentiated muscular tissue and the lumen, already S-shaped owing to the development of the two main muscular pillars, was lined with a cuboidal epithelium with central nuclei. Of the female system at this stage little can be said. The uterus and vagina are present as tubes lined by a uniform epithelium. The albumen gland is entirely undeveloped, likewise the muciparous and oöthecal glands. The receptaculum seminis and its duct are present but the receptacle sac is scarcely more than a slight dilatation of the duct. The only evidence of differentiation in the female tract in this specimen is that the nuclei of the epithelial cells in the regions that will become glandular stain more deeply in haematoxylin than do those of the other regions.

The gonad of the "adolescent" snail (5.7 mm. shell length) showed clusters of mature spermatozoa in the acini with a few maturing oöcytes in the upper parts. Some of the largest of these oöcytes showed dividing nuclei and were, presumably, undergoing maturation division. Sections of the seminal vesicle and hermaphrodite duct were packed solidly with spermatozoa. The sperm duct after its separation from the common duct shows the same short, ciliated part followed by the long, glandular part with refractile eosinophil granules in the cytoplasm as is found in the adult. The prostate gland also is identical histologically to the adult. Throughout its course the vas deferens corresponds in histological detail to the form already described in the adult. The transition to the epiphallus is similar as are the structures of the penis and penis sheath. The preputium, however, is, in its distal part, similar to that in the juvenile in that the lumen is S-shaped and only two muscular pillars are present. More proximally additional folds in the wall do occur. The epithelium lining the lumen is more ciliated than in the adult and few gland cells have been

observed. The female tract at this stage is far less well developed. The albumen gland is represented by a fairly compact mass of tissue of undoubtedly glandular nature but scarcely organized into tubules as in the adult. The few tubules which are present are not lined with the characteristic glandular epithelium of the adult but with cells which probably later develop into this form. The carrefour is present as a dilatation of the oviduct but its epithelial lining is only differentiated into glandular areas in parts, some cilia are also present. The oviduct is similar histologically to that in the adult and it in turn passes into the ciliated part of the uterus. Neither the muciparous nor the oöthecal glands is represented by more than a slight thickening of the uterine wall. The receptaculum seminis is well developed and contains spermatozoa and the vagina is strongly ciliated.

These histological observations support the opinion already formed from gross anatomical studies that the male genital tract develops slightly earlier than the female system. Morton (1954) has suggested that a protandrous sexual cycle is the primitive condition in gastropods and that simultaneous hermaphroditism has been later developed in the higher pulmonates and opisthobranchs. Larambergue (1939) states that in *Bulinus contortus* there is no protandry since spermatozoa and ova are produced simultaneously throughout life even though spermatozoa do appear first. It seems probable that the earlier development of the male tract is a relic of the primitive protandrous condition which has become almost completely obscured, particularly where the length of the breeding season is limited by adverse environmental conditions.

To complete this histological study of the genital organs of *B. jousseaumei* a few comparisons with similar studies on related forms should be considered. It has already been said that there are no differences between the fundamental structure of the gonad in this species and in *Biomphalaria boissyi* and *Helisoma trivolvis* as described by Abdel-Malek (loc. cit.) and it is probable that this structure is fairly uniform throughout the Planorbidae. The hermaphrodite duct corresponds to the description by Larambergue (loc. cit.) for that in *B. contortus*, also the point of separation of the male and female tracts. The sperm duct differs from that in *B. contortus* in that no ciliation has been observed in its lumen apart from the very short part immediately after its separation from the common duct. Abdel-Malek mentions no ciliation of the sperm duct in *B. boissyi* and only near the prostate in *H. trivolvis*. In both of these species he mentions the refractile, eosinophilic, cytoplasmic granules but also records the presence of scattered basophils not seen in *B. jousseaumei*. The prostate corresponds well with that described by Larambergue for *B. contortus* and this author stresses the fact that the gland is not traversed by the male duct but that its tubules open into a central chamber into which the sperm duct opens at one side and from which the vas deferens leaves at the other. The vas deferens in *B. jousseaumei* differs from that in *B. contortus* in that it is ciliated throughout its length while Larambergue reports that in the second species the epithelium is unciliated and of a mucous-secreting type. In both of the species described by Abdel-Malek the vas deferens is ciliated throughout its length although, due to the different form of the prostate in these species, there is only a gradual transition from the form of the sperm duct to that of the vas deferens instead of a

clear-cut demarcation of the two as in *B. jousseaumei*. The epiphallus which is so well differentiated from the vas deferens in the present species was also noted (although not under this name) by Larambergue to be histologically different. Since the structure of the copulatory apparatus in the species described by Abdel-Malek differs so markedly from that in the Bulinids it is not possible to draw comparisons between the histology of the two but it is interesting to note that in his species the seminal canal within the penis (and therefore that part of the male duct actually inside the penis sheath) is ciliated and that the epithelial lining does not differ from that of the vas deferens. The histological structure of the penis, penis sheath and preputium in the present species show no significant differences from those described by Hubendick (1948b) and Larambergue. Larambergue does not describe the histology of the female genital tract of *B. truncatus* apart from mentioning the ciliation of the receptaculum seminis duct. The epithelial linings of the first part of the oviduct and of the carrefour are similar to those of *B. boissyi* and *H. trivolvis* although not so heavily ciliated. Beyond the carrefour the epithelium of the oviduct in the present species almost entirely lacks cilia while these are present in *Biomphalaria*. The epithelium of the uterus is similar in the two species, and the muciparous gland merges gradually with the uterus rather than abruptly as in *Helisoma*. The remainder of the female tract is very similar to *Biomphalaria* except that the part of the receptaculum seminis duct nearest to the vagina is unciliated, a condition similar to that in *Helisoma*.

RELATIONSHIPS OF *B. JOUSSEAUMEI*

In considering the affinities of *B. jousseaumei* it is necessary to review the species of the sub-genus *Physopsis* known from West Africa. For this purpose it is often necessary to refer to the medical literature as it is largely in works on the epidemiology and transmission of human schistosomiasis that records of intermediate hosts are to be found. The only species of *Physopsis* actually described from West Africa is *P. globosa* (Morelet, 1866) collected in Angola. Of the other twenty or so species, all were described originally from East or South Africa. The question of the identity of *P. globosa* with *P. africana* Krauss, 1848, will not be dealt with here since opinions are still divided on this point and much detailed work must be carried out before a solution of the problem can be reached. It must, however, be pointed out that many authors now treat *P. globosa* as an absolute synonym of *P. africana* others consider it to be a variety or sub-species of the latter while still others recognize it as a separate species. In the following account it will be pointed out (where it is known) which of these three courses was adopted by the workers concerned. Since a chronological account of these records would undoubtedly prove confusing, they are presented in a geographical sequence from north to south.

McCullough & Duke (1954) were the first to record *Bulinus africanus* from the Gambia and they noted that this was probably the northernmost record for the species in West Africa. They were following the classification of Amberson & Schwarz (1953) who treated all species of *Physopsis* as forms of *B. africanus* and there is no doubt that their record refers to *B. jousseaumei*. I later recorded (Wright,

1956) a form of *B. (P.) globosus* from one locality in Upper River Division, Gambia, as well as *B. jousseaumei* from the Casamance Province of Senegal, the next territory to the south of the Gambia. No published records of *Physopsis* from Portuguese Guinea have been found, and Pinto (1949) in a recent survey of vesicle schistosomiasis in that territory found only *Bulinus forskali* and *B. dautzenbergi*. Vogel (1932) in a similar survey in French Guinea and Liberia found (and illustrated) *Physopsis globosa*. More recently in a rather confusing account of schistosomiasis in French West Africa, Le Gall (1944) mentions as a probable vector of urinary schistosomiasis in French Guinea "*Physopsis ovooides* and *boissyi*" from Kissidougou. This presumably refers to *P. ovoideus* and *Biomphalaria boissyi*. The next territory southwards from the French Guinea coast, Sierra Leone, is perhaps one of the best documented areas in tropical Africa with respect to the epidemiology of schistosomiasis. It has been the subject of three major surveys. Blacklock (1924), Blacklock & Thompson (1924), Blacklock (1925), Gordon, Davey & Peaston (1934) and Gerber (1952). Connolly (1928) published an account of the freshwater molluscan material collected by Blacklock and considered the *Physopsis* to be *P. globosa* with strong affinities to *P. didieri*. He mentioned the presence of a well-marked spiral sculpture on the material from Sierra Leone, a feature which he had not observed on *P. globosa* from Angola and Mozambique. Connolly also identified material submitted to him by Gordon and his co-workers and identified the *Physopsis* as *P. globosa*. Gerber submitted his material to Dr. W. J. Rees who identified one fully-grown and three smaller specimens out of a batch of 204 shells as *Bulinus globosus* and referred the remaining 200 to *B. africanus*. The same sample of shells was shown to Berry who pronounced them all to be *Physopsis africana*. To the south of Sierra Leone is Liberia and here Vogel (loc. cit.) records *Physopsis globosa* and Veatch (1946) mentions *Physopsis africana* var. *globosa* as the intermediate host of *Schistosoma haematobium* in the Western Province. No records of identified *Physopsis* from the Ivory Coast have been seen but Ingram (1924) incriminated *P. globosa* as the possible vector of urinary schistosomiasis in the Gold Coast; more recently Edwards & McCullough (1954) have demonstrated that the parasite is carried by *P. africana* but they also mention that they consider *P. globosa* to be either a race or an absolute synonym of this species. The only further record of an identified *Physopsis* between the Gold Coast and the Belgian Congo is that of *P. globosa* collected at Kano in Northern Nigeria (Gordon, 1932). In the excellent work of Pilsbry & Bequaert (1927) a variety of *P. africana* is recorded from a number of localities in the Belgian Congo, also *P. africana globosa*. These authors refer the other recorded species of *Physopsis* (apart from *P. tanganyicae* von Martens) from the Belgian Congo either to *P. africana* var. or to *P. africana globosa*. Finally, the territory to the south of the Belgian Congo, Angola, is the type locality for *P. globosa* Morelet.

Examination of material from French Guinea, Sierra Leone, Liberia, Belgian Congo and Angola has shown that without doubt the same species of *Physopsis* is present in all these territories and that *B. jousseaumei* is a form of that species. The table below gives the mean dimensions in millimetres of the populations examined from the territories mentioned above :

Territory and number of specimens	Shell length	Shell		Aperture length	Aperture width	Shell length	
		max. diam.	Aperture length			Aperture width	Aperture length
Gambia 283	7.84 . ±1.52	6.00 . ±1.12	6.65 . ±1.03	3.37 . ±0.66	2.31 . ±0.14	1.17 . ±0.08	
Casamance 20	8.69 . ±0.96	6.32 . ±0.76	7.21 . ±0.70	3.60 . ±0.33	2.41 . ±0.13	1.20 . ±0.04	
French Guinea 20	10.33 . ±0.75	7.01 . ±0.42	8.31 . ±0.51	4.04 . ±0.20	2.55 . ±0.11	1.24 . ±0.05	
Sierra Leone 100	10.07 . ±2.06	7.18 . ±1.75	8.43 . ±1.43	3.97 . ±0.93	2.55 . ±0.19	1.19 . ±0.08	
Liberia 6	10.56 . ±2.81	7.38 . ±1.63	8.8 . ±1.98	4.28 . ±1.06	2.47 . ±0.15	1.19 . ±0.07	
Belgian Congo 100	11.34 . ±1.64	8.50 . ±1.22	9.51 . ±1.52	4.54 . ±0.63	2.48 . ±0.11	1.19 . ±0.065	
Angola (Type series) 26	13.43 . ±2.19	9.51 . ±1.63	9.60 . ±1.48	5.13 . ±0.85	2.62 . ±0.15	1.40 . ±0.085	

Text-fig. 26 shows the means for the ratio Shell length/Aperture length plotted against the mean lengths for each of these samples. Text-figs. 27-30 show the ratios shell length/aperture length and the frequency distributions of shell length in the samples from Sierra Leone and the Belgian Congo.

Reference to the table shows a gradual decrease in the dimensions of the shell from south to north. The composition of the samples is not wholly comparable, those from the Gambia, Sierra Leone and Belgian Congo are more or less random population samples with a proportion of juveniles and those from Casamance, French Guinea and the type series from Angola contain mostly adult specimens. The small sample from Liberia consisted of four adults and two juveniles, hence the rather large standard deviations. The means of the type series differ from those given by Mozeley (1939) because his figures were based on ten specimens of the series only. In addition to the discrepancies in sampling certain differences due to ecological conditions also occur. The most obvious of these is the "still water" effect. Schwetz (1954) has described the effect of changed environment on shell form in several planorbid snails and the exertion of the spire in forms which develop in static water compared to those in gently moving streams is well known. This accounts largely for the difference in the mean values of the ratio shell length/aperture length in the type series and in the Belgian Congo sample. The latter came from a pool in a recently dried stream bed while Morelet (1868) notes that the Angolan material was collected in a lake. Similarly this probably accounts for some of the differences between Gerber's and Blacklock's specimens from Sierra Leone. Gerber's material from the still waters of a rice swamp has a more exerted spire than Blacklock's from a stream,

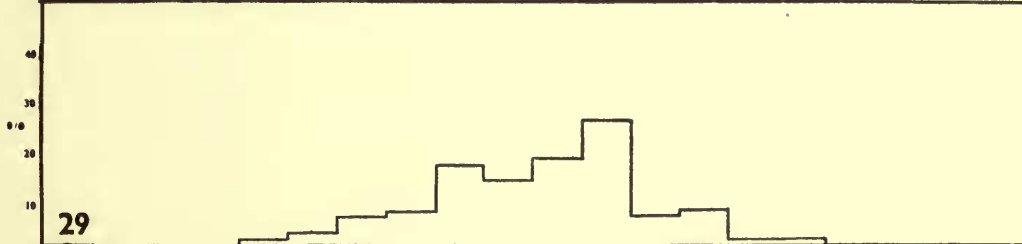
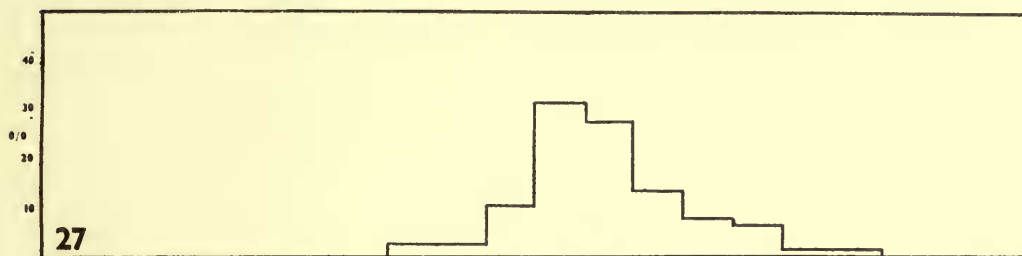
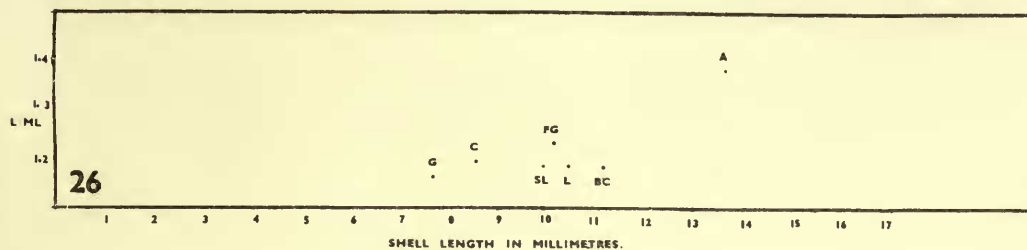


FIG. 26. Graph of mean ratio shell length/aperture length against mean shell length for populations of *B. jousseaumei* from Gambia (G), and Casamance (C) and *B. globosus* from French Guinea (FG), Sierra Leone (SL), Liberia (L), Belgian Congo (BC) and the type series from Angola (A).

FIG. 27. Size-frequency histogram for a population of *B. globosus* from Belgian Congo.

FIG. 28. Graph of ratio shell length/aperture length against shell length for the same population.

FIG. 29. Size-frequency histogram for sample of *B. globosus* from Sierra Leone.

FIG. 30. Graph of shell length/aperture length against shell length for the same population.

The general form of the shell is similar throughout the whole range under consideration (Plate I). In the same population shells may be seen with the columella margin fused entirely to the body whorl and others with a space between the two. This was stressed by Connolly (1934) as being the only constant conchological difference between *Physopsis africana* and *P. globosa*. There is also a range of variation in the angle at which the outer lip meets the body whorl at the top of the aperture, a character used by Pilsbry & Bequaert (1927) for the separation of the same two species. The sculpture pattern described earlier for the Gambian material is found also throughout the range, being most marked in the specimens from Sierra Leone (Plate 2,) and, as noted by Connolly (1928) practically absent from the Angolan material. This is of interest since Mandahl-Barth (1954) erected a sub-species *Bulinus globosus ugandae* which he separated from the nominate sub-species because it completely lacked the spiral sculpture of the typical form. In passing it seems appropriate to note that amongst the shells collected in Northern Rhodesia by Buckley (1946) were a number of specimens labelled by Connolly as juvenile *Bulinus natalensis* but which were also referable to *B. hemprichii depressus* Haas, 1936. These specimens were indistinguishable from many of the juvenile *Physopsis globosa* seen during this work. Unfortunately the type specimens of Haas' subspecies were destroyed or lost during the war but from a study of the photographs of these specimens there can be little doubt that the sub-species should be placed in the synonymy of *Bulinus (Physopsis) globosus*.

It can be seen from Text-fig. 30 that the pattern of the graph of shell length/aperture length against shell length for the sample from Sierra Leone is similar to that for the Gambian population (Text-fig. 3). For the lower values of shell length the graph is almost parallel to the horizontal axis and the gradual upward slope does not begin until a shell length of about 8.0 mm. is reached. It has already been shown that this change is brought about by the onset of the adult phase and it should be noted that it occurs at a greater shell length in the Sierra Leone population than

FIGS. 31-35. Stages in the development of the accessory genital glands and male copulatory organ of *B. jousseaumei* from the Gambia.

Fig. 31 at 4.5 mm. shell length.

Fig. 32 at 5.2 mm. shell length.

Fig. 33 at 6.3 mm. shell length.

Fig. 34 at 7.5 mm. shell length.

Fig. 35 at 8.8 mm. shell length.

FIGS. 36-38. Stages in the development of the accessory genital glands and male copulatory organ of *B. globosus* from Sierra Leone.

Fig. 36 at 6.1 mm. shell length.

Fig. 37 at 8.5 mm. shell length.

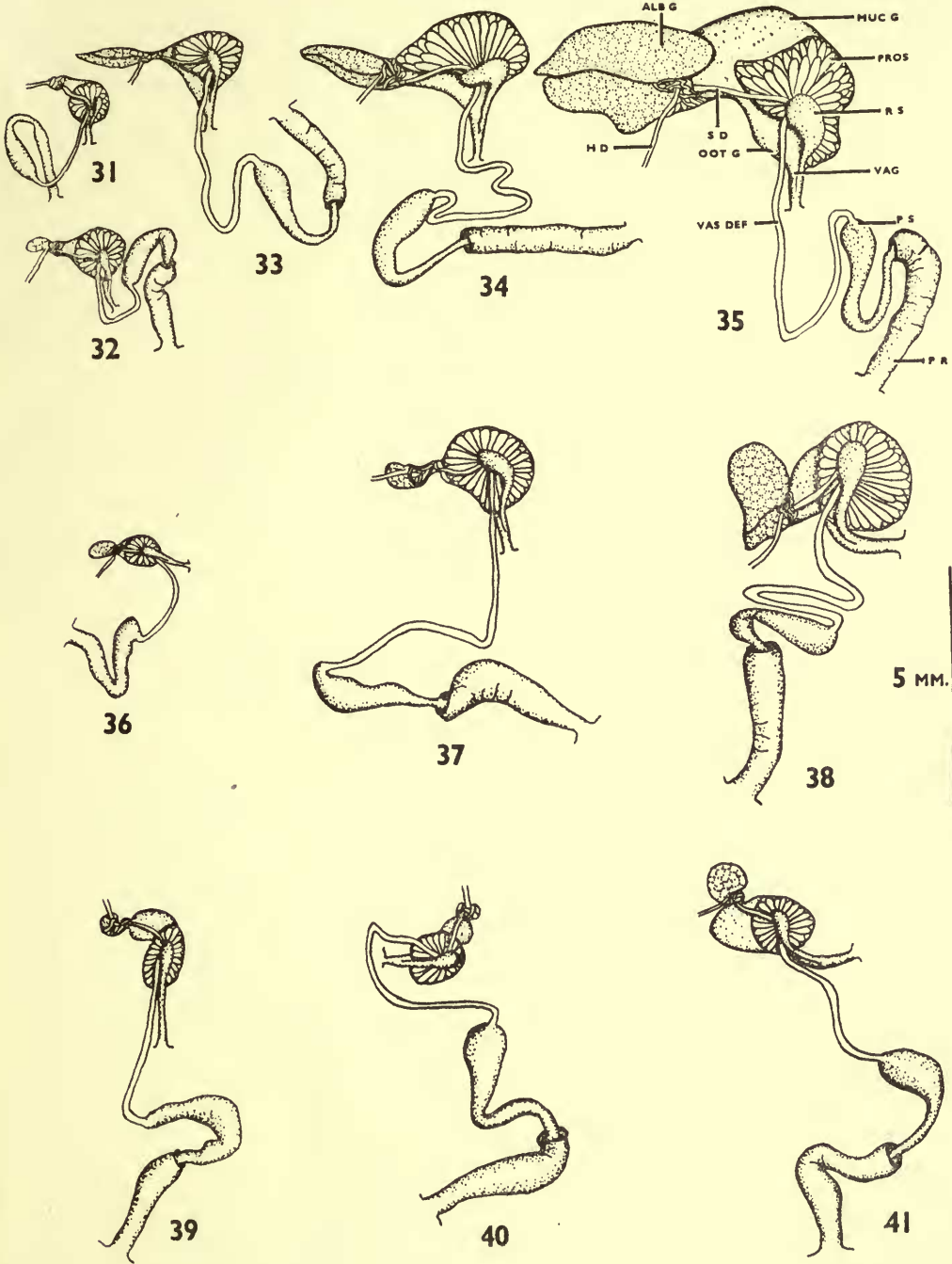
Fig. 38 at 9.2 mm. shell length.

FIGS. 39-41. Similar stages in *B. globosus* from Angola.

Fig. 39 at 8.9 mm. shell length.

Fig. 50 at 9.5 mm. shell length.

Fig. 41 at 9.75 mm. shell length.



in that from the Gambia. That the same characteristic is present in the corresponding graph for the Belgian Congo material is almost certain; the distribution of individuals in the sample is, however, such that the feature is not well marked although it seems probable that it occurs at an even greater size than in the Sierra Leone population.

Although no anatomical differences in structure have been found in the limited material examined (Sierra Leone, Belgian Congo and Angola) there is a variation in degree of development of the genital organs at corresponding shell sizes. Text-figs. 31-35 show stages in the development of the accessory genital glands and male copulatory organ at various shell lengths for *B. jousseaumei* in the Gambia. Text-figs. 36-38 are of three stages in *B. globosus* from Sierra Leone and Text-figs. 39-41 for material from Angola. The degree of development of the Gambian specimen of 5.2 mm. shell length (Text-fig. 32) compares well with that of 8.5 mm. from Sierra Leone (Text-fig. 37) and 9.5 mm. from Angola (Text-fig. 40). The protandrous development of the male copulatory organ and prostate is even better marked in these last two groups of specimens than it is in *B. jousseaumei*.

Of possible significance, but at present insufficiently investigated, is the increased pigmentation of the mantle in the more southern forms. Specimens from Sierra Leone and the Belgian Congo have the mantle heavily blotched with black in contrast to the more diffuse spotting of that in *B. jousseaumei*. Three of the four specimens dissected from Angola had almost the entire mantle black with one or two lighter patches.

Differences in the radula do not seem significant; one or two more laterals in each transverse half row may be found in the larger forms but this is to be expected.

DISCUSSION

Evidence has been presented to show that *Bulinus jousseaumei* from the Senegambian region is closely related to the other species of the sub-genus *Physopsis* from neighbouring West African territories and that these in turn are related to the typical *Bulinus globosus*. In spite of a number of distributional gaps, probably due to an absence of collectors rather than of snails, it seems clear that there is a well-marked cline grading from the typical *globosus* form in the south to the small *jousseaumei* at the extreme northern limit of the range. Not only is this cline represented by a gradation in size but also by a gradation in the degree of protandric development, possibly also by differences in the intensity of mantle markings. The change does not become really well marked until (moving northward) Sierra Leone is reached. It seems very probable that the cline is correlated with the length of the rainy season. In the Senegambian region there is a single wet season of about four months duration while to the south the season is prolonged and may be duplicated. The short single wet season will limit the time during which the streams and bolons are suitable for the development of snails, hence the telescoping of the sexual phases and the reaching of sexual maturity at a smaller shell size. In regions of more continuous rainfall the need for rapid development is less, resulting in the more marked protandrous development (a primitive character) and the later

onset of sexual maturity, the latter being of course closely connected with the larger shell size.

Although the use of a trinomial system of nomenclature is of doubtful value unless it is well documented it seems justifiable to retain the name *jousseaumei* as a sub-species in this case, for the Senegambian form. It differs from the typical form of *globosus* in its considerably smaller size and its apparently more contracted life cycle. It is at present geographically isolated from the typical form by the distributional gap in Portuguese Guinea but subsequent work may well show that this is not actually so. The name *Bulinus (Physopsis) globosus jousseaumei* (Dautzenberg) is therefore proposed.

If *B. jousseaumei* is a sub-species of *B. globosus* then the problem of its affinities with the strongly umbilicate form of *B. globosus* described from the Gambia (Wright, 1956) arises since two geographical races of the same species are not to be expected in the same geographical region. In this form the columellar margin of the aperture is greatly developed and not reflected, giving rise to a wide umbilicus with a slight keel around its opening. The columellar truncation is also thus suppressed leaving only a thickened line on the inner surface of the columella. There appears to be no record in the literature that the type series of *B. globosus* includes several specimens which show this character in a very limited degree. Material in a collection made in Northern Rhodesia by Dr. P. Le Roux contains a number of specimens which show this character even further developed. Intermediate forms between the Rhodesian and Gambian specimens have been seen in Blacklock's collection from Sierra Leone. In these the umbilicus is well developed but not quite so wide as in the Gambian material. Although the evidence is incomplete it appears that this variety of *B. globosus* also shows a clinal distribution parallel to that described for the typical form and *B. jousseaumei*. In this instance the main character in which gradation has been observed is in the degree of overgrowth of the columellar margin with consequent suppression of the columellar truncation and increase in the size of the umbilicus. Insufficient spirit material has been available for a study of associated anatomical variation. The only locality from which this umbilicate form was obtained in the Gambia was at Badja Kunda, Upper River Division where the ecological conditions differed slightly from those in the typical *B. jousseaumei* habitats. A single specimen of *B. jousseaumei* showing this character slightly developed was obtained with normal specimens at Sudowol bridge over the Simoto bolon, Upper River Division. The evidence suggests that this is possibly a recessive genetic character of the normal form which, when it occurs as a pure homozygous population is better adapted to slightly different habitats and appears to behave as a separate species.

SUMMARY

1. A brief biometrical study of the shell of *B. jousseaumei* is made.
2. The histology and course of development of the genital tract of this snail is described and compared with related planorbids.
3. The records of *Physopsis* spp. from West Africa are briefly surveyed. The possibly fallacious premises on which *Bulinus globosus ugandae* Mandahl-Barth

was described are mentioned and *Bulinus hemprichii depressus* Haas is referred to the synonymy of *B. globosus*.

4. The relationship of *B. jousseaumei* to *B. globosus* is discussed and the former is reduced to a sub-species of the latter as *B. g. jousseaumei*, the northernmost representative of a cline of the typical form.

5. The relationship of *B. g. jousseaumei* to the umbilicate form of *B. globosus* is discussed and this form is related through a graded series to the typical form.

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REFERENCES

- ABDEL-MALEK, E. T. 1954a. Morphological studies on the family Planorbidae (Mollusca : Pulmonata). I. Genital organs of *Helisoma trivolvis* (Say) (Subfamily Helisomatinae F. C. Baker, 1945). *Trans. American Microscopical Soc.* **73** (2) : 103-123.
- 1954b. Morphological studies on the family Planorbidae (Mollusca : Pulmonata). II. The genital organs of *Biomphalaria boissyi* (Subfamily Planorbinae, H. A. Pilsbry 1934), *Ibid.* **73** (3) : 285-296.
- AMBERSON, J. M. & SCHWARZ, E. 1953. On African Schistosomiasis. *Trans. Roy. Soc. Trop. Med. Hyg.* **47** (6) : 451-502.
- BLACKLOCK, D. B. 1924. Report of an investigation into the prevalence and transmission of human schistosomiasis in Sierra Leone. *Sierra Leone Ann. Med. San. Rep. for 1923* : 80-87.
- 1925. Endemic goitre and schistosomiasis in Sierra Leone. *Trans. Roy. Soc. Trop. Med. Hyg.* **18** (8) : 395-427.
- & THOMPSON, M. G. 1924. Human schistosomiasis due to *S. haematobium* in Sierra Leone. *Ann. Trop. Med. & Parasit.* **18** (2) : 211-234.
- BUCKLEY, J. J. C. 1946. A helminthological survey in Northern Rhodesia. *J. Helminthology*, **21** (4) : 111-174.
- CONNOLLY, M. 1928. The non-marine mollusca of Sierra Leone. *Ann. Mag. Nat. Hist. Series 10*, **1** (4) : 529-551.
- 1934. On the planorbid hosts of bilharziasis in South and West Africa. *Ann. Trop. Med. & Parasit.* **28** (3) : 439-443.
- DAUTZENBERG, P. H. 1890. Récoltes malacologiques de M. le capitaine Em. Dorr, dans le Haut-Senegal et le Soudan Français de 1886-1889. *Mem. Soc. Zool. France*, **3** : 132-134.
- DESCHIENS, R. 1951. Le problème sanitaire des bilharzioses dans les territoires de l'Union Française. *Bull. Soc. Path. Exot.* **44** : 631-638.
- DUPUIS & PUTZEYS. 1923. Deuxième note concernant le Faune Malacologique Africaine. *Ann. Soc. Zool. et Malac. Belgique*, **53** : 69-79.
- EDWARDS, E. E. & McCULLOUGH, F. S. 1954. Studies on the life cycles of *Schistosoma haematobium* and *S. mansoni* in the Gold Coast. *Ann. Trop. Med. and Parasit.* **47** : 164-177.
- GERBER, J. H. 1952. Bilharzia in Boajibu. Part 1. *J. Trop. Med. & Hyg.* **55** (3) : 52-58.
- 1952. Bilharzia in Boajibu. Part 2. *Ibid.* **55** (4) : 79-93.

- GORDON, R. M. 1932. The molluscan host of *Schistosoma haematobium* in Northern Nigeria. *Ann. Trop. Med. & Parasit.* **26** : 117-118.
- DAVEY, T. H. & PEASTON, H. 1934. The transmission of human bilharziasis in Sierra Leone, with an account of the life-cycle of the schistosomes concerned, *S. mansoni* and *S. haematobium*. *Ibid.* **28** (3) : 323-418.
- HAAS, F. 1936. Binnen-Mollusken aus Inner Afrika. *Abh. Senckenberg. Naturf. Ges.* **431** : 1-156. Frankfurt A.M.
- HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J.M.B.A.* **28** : 141-153.
- HUBENDICK, B. 1948a. The Anatomy of *Bulinus*, with a discussion of the term prostate and its sense in the Basomatophora. *Proc. Malac. Soc. Lond.* **27** (5) : 186-196.
- 1948b. Studies on *Bulinus*. *Ark. för zoologi*, **40A** (16) : 1-63.
- 1951. Recent Lymnaeidae. *Kungl. Svenska Vetenskap. Hand.* Fjärde Serien, **3** (1) : 1-223.
- INGRAM, A. 1924. Note on a possible intermediate host of *Schistosoma haematobium* in the Gold Coast. *Ann. Trop. Med. & Parasit.* **18** (3) : 265-266.
- LARAMBERGUE, M. DE. 1939. Etude de l'autofécondation chez les gasteropodes pulmonés. Recherches sur l'aphallie et la fécondation chez *Bulinus (Isidora) contortus* Michaud. *Bull. Biol. Paris*, **73** : 1-231.
- LE GALL, R. 1944. Les bilharzioses en Afrique Occidentale Française au Togo et a Madagascar de 1939a 1941. *Bull. Off. Int. d'Hyg. Pub.* **36** : 116-126.
- MANDAHL-BARTH, G. 1954. The freshwater mollusks of Uganda and Adjacent territories. *Ann. Mus. Roy. Congo Belge Tervuren, Serie in 8°*, Sciences zoologiques 32.
- MCCULLOUGH, F. S. & DUKE, B. O. L. 1954. Schistosomiasis in the Gambia. 1. Observations on the potential snail vectors of *Schistosoma haematobium* and *S. mansoni*. *Ann. Trop. Med. & Parasit.* **48** (3) : 277-286.
- MEEUSE, A. D. J. 1950. Rapid methods for obtaining permanent mounts of radulae. *Bacteria*, **14** (2 & 3) : 28-43.
- MORELET, A. 1866. Coquilles nouvelles recueillies par le Dr. Fr. Welwitsch dans l'Afrique équatoriale et particulièrement dans les provinces portugaises d'Angola et de Benguela. *J. de Conchyliologie*, **14** : 153-163.
- 1868. Mollusques terrestres et fluviatiles. *Voyage du Dr. Friederick Welwitsch*, Paris.
- MORTON, J. E. 1954. The pelagic mollusca of the Benguela Current. With an account of the reproductive system and sexual succession of *Limacina bulimoides*. *Discovery Reports*, **27** : 163-200.
- MOZELEY, A. 1939. The freshwater mollusca of the Tanganyika Territory and Zanzibar Protectorate and their relation to human schistosomiasis. *Trans. Roy. Soc. Edinburgh*, **59** (3) : 687-744.
- PETERS, B. G. 1938. Biometrical observations on shells of *Limnaea* Species. *J. Helminth.* **16** (4) : 181-212.
- PILSBRY, H. A. & BEQUAERT, J. 1927. The aquatic molluscs of the Belgian Congo. *Bull. Amer. Mus. Nat. Hist.* **53** (2) : 69-602.
- PINTO, A. R. 1949. Os primeiras dados sobre a existencia da Schistosomiasse vesical na Guiné Portuguesa e importancia da contagem de ovas do parasito no sedimento urinario. *Anais. Inst. Med. Trop.* Lisboa **6** : 75-114.
- SCHWETZ, J. 1954. L'influence du milieu sur la taille et la forme du même Planorbe ou du même *Bulinus*. *Ann. Soc. Roy. Zool. Belge*, **85** (1) : 23-34.
- SMITHERS, S. R. 1956. On the ecology of schistosome vectors in the Gambia with evidence of their rôle in transmission. *Trans. Roy. Soc. Trop. Med. & Hyg.* **50** (4) : 354-365.
- VEATCH, E. P. 1946. Human trypanosomiasis in Liberia 1941-44. Supplement to *Amer. J. Trop. Med.* **26** (5) : 1-56.
- VOGEL, H. 1932. Beitrage zur epidemiologie der schistosomiasis in Liberia und Französisch-Guinea. *Arch. Schiffs-u. Tropenhyg.* **36** (3) : 108-135.

- WATSON, H. (In CONNOLLY, M.). 1925. The non-marine mollusca of Portuguese East Africa. *Trans. Roy. Soc. S. Africa*, 12 (3) : 105-220.
- WRIGHT, C. A. 1956. The anatomy of six species of the Molluscan genus *Bulinus* (Planorbidae) from Senegambia. *Proc. Malac. Soc. Lond.* In press.

ABBREVIATIONS USED IN FIGURES

FIGS. 5 & 6.—

BUC	= buccal ganglion.
CER	= cerebral ganglion.
OT	= otocyst.
OT N	= otocyst nerve.
PED	= pedal ganglion.
PEN N	= penial nerve.
PL	= pleural ganglion.
VIS	= visceral ganglion.

FIG. 7.—

CAE	= caecum.
CRO	= crop.
GIZ	= gizzard.
INT	= intestine.
STO	= stomach.

FIG. 35.—

ALB G	= albumen gland.
H D	= hermaphrodite duct.
MUC G	= muciparous gland.
OOT G	= oöthecal gland.
P R	= preputium.
PROS	= prostate.
P S	= penis sheath.
R S	= receptaculum seminis.
S D	= sperm duct.
VAG	= vagina.
VAS DEF	= vas deferens.

